Proc. Kon. Ned. Akad. v. Wetensch. 100 (1-2), 141–160 June 23, 1997

# On *Bunolistriodon* (= *Eurolistriodon*) and Kubanochoeres

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Communicated by Prof. J.E. van Hinte at the meeting of June 23, 1997

## ABSTRACT

The name *Eurolistriodon* Pickford and Moyà-Solà, 1995 was meant to replace *Bunolistriodon*, for a wide-spread group of Miocene pigs. However, *Bunolistriodon* Arambourg 1963 is a valid name, and thus *Eurolistriodon* is a junior synonym.

Three groups of derived characters are shared by kubanochoeres and listriodonts: 1) meso-distal diameter of the incisors and related characters such as anterior mandible shape, 2) decrease in the height of the crown of the incisors, and 3) the morphology and the orientation of the first upper incisor. These characters show that the kubanochoeres belong to the Listriodontinae, though most of the characters tend to be more developed in the Listriodontini than in the Kubanochoerini.

## INTRODUCTION

Unfortunately the classification of the Listriodontinae suffered from instability during the last twenty years. Wilkinson (1976) placed a number of listriodontine suids in the genus *Bunolistriodon*, Wilkinson (1978) placed these species in *Kubanochoerus* and Pickford (1986) placed them in *Libycochoerus*. Savage (1990, p. 593), reviewing African faunas, complained: 'However, the taxonomic identity of African suids (and anthracotheres) is very shaky; every paper published in recent years has produced yet another horrendous change of names and the synonomy now surpasses that of any other mammalian stock on the continent. A careful and responsible taxonomic revision for both suids and anthracotheres is sorely needed.' A classification of the Suidae at the genus level is presented in figure 1 and figure 2 gives the stratigraphical position of the type

Family Suidae

| Subfamily | Tribe | Genus | Selected synonyms |
|---|---|---|---|
| Cainochoerinae | | | |
| | | *Kenyasus* | |
| | | *Albanohyus* | *Barberahyus* |
| | | *Cainochoerus* | |
| Listriodontinae | | | |
| | Namachoerini | | Lopholistriodontini,<br>Namachoerinae |
| | | *Nguruwe* | |
| | | *Lopholistriodon* | *Namachoerus* |
| | Kubanochoerini | | Kubanochoerinae |
| | | *Kubanochoerus* | *Libycochoerus* |
| | Listriodontini | | |
| | | *Bunolistriodon* | *Eurolistriodon* |
| | | *Listriodon* | *Callydonius*,<br>*Tapirotherium*,<br>*Lophiochoerus* |
| Hyotheriinae | | | |
| | | *Aureliachoerus* | |
| | | *Xenohyus* | |
| | | *Hyotherium* | |
| | | *Chleuastochoerus* | |
| Tetraconodontinae | | | |
| | | *Parachleuastochoerus* | |
| | | *Conohyus* | |
| | | *Nyanzachoerus* | |
| | | *Notochoerus* | |
| | | *Lophochoerus* | |
| | | *Sivachoerus* | |
| | | *Tetraconodon* | |
| Suinae | | | |
| | Babirusini | | Potamochoerinae |
| | | *Celebochoerus* | |
| | | *Potamochoerus* | |
| | | *Babyrousa* | |
| | Phacochoerini | | Hippohyini |
| | | *Sivahyus* | |
| | | *Hippohyus* | |
| | | *Metridiochoerus* | |
| | | *Potamochoeroides* | |
| | | *Phacochoerus* | |
| | Dicoryphochoerini | | |
| | | *Propotamochoerus* | *Korynochoerus* |
| | | *Hippopotamodon* | *Microstonyx* |
| | | *Eumaiochoerus* | |
| | | *Kolpochoerus* | *Mesochoerus* |
| | | *Hylochoerus* | |
| | Suini | | |
| | | *Sus* | *Porcula* |

Fig. 1. A classification of the Suidae.

material of each species (dots) and the phylogenetic relationships of the Listriodontinae (modiefied after Van der Made, 1996).

In a recent paper, Pickford and Moyà-Solà (1995), introduced the new name

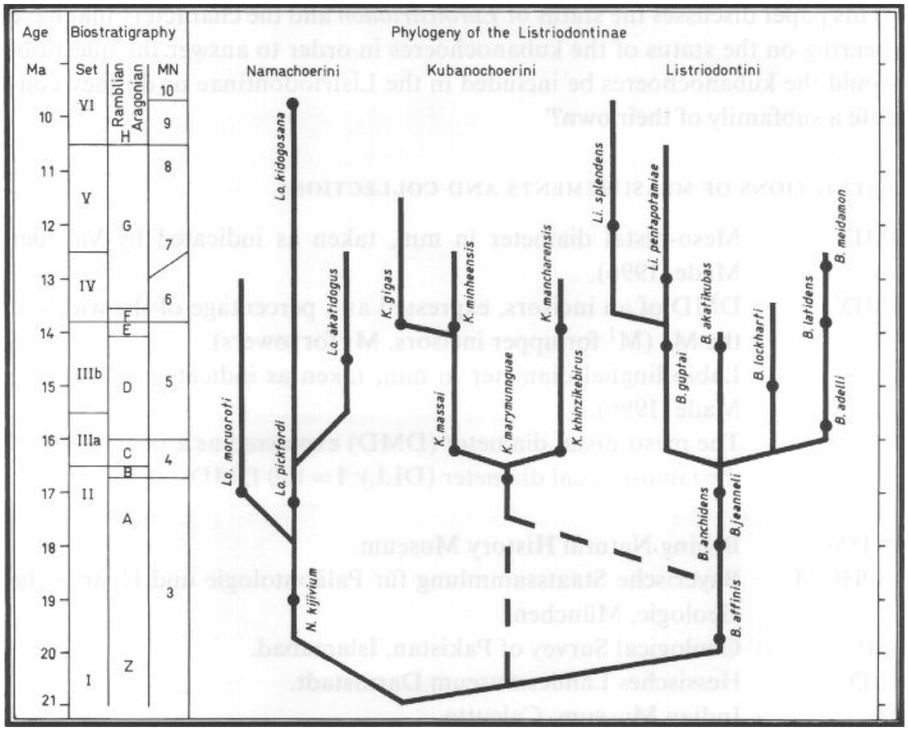

Fig. 2. The evolution and stratigraphical position of the type material (dots) the Listriodontinae. Stratigraphy modified after Alvarez Sierra et al. (1997) and Van der Made (1996). Sets are Faunal Sets of Pickford (1981) for Africa, Ramblian and Aragonian biozones from various papers by Daams, Alvarez Sierra and Freudenthal, and MN Neogene Mammal units from Mein (1975, 1990) and De Bruijn et al. (1992). Namachoerini are known from Africa, *K. minheensis* from China, *K. robustus* from China, Russia and the Indian Subcontinent, *K. mancharensis* from Turkey and the Indian Subcontinent, remaining *Kubanochoerus* spp. from Africa, *L. splendens* and possibly *B. lockharti* (= ? *B. intermedius*) from Europe and China, *B. adelli – meidamon* lineage from Europe and Turkey, *B. guptai – L. pentapotamiae* from the Indian Subcontinent, the *B. affinis – jeanneli* lineage from Africa and the Indian Subcontinent and *B. akatikubas* from Africa.

*Eurolistriodon* to replace the widely used name *Bunolistriodon*. They state that *Bunolistriodon* is a nomen nudum and include *B. lockharti*, type species of *Bunolistriodon* in *Eurolistriodon*. They further introduced a new species, *E. adelli* on the basis of a comparison of the material from Els Casots with that from Can Canals, but omit a comparison with the types of *B. lockharti* and *B. belsiacus*. The absence of $P^2$ and $P_2$ in the type of *B. adelli* is probably pathological and *B. adelli* might be identical to *Bunolistriodon* aff. *latidens* of Van der Made (1996) and be ancestral to *B. latidens*.

Pickford (1986, 1988, 1995) and Pickford and Moyà-Solà (1995) included *Kubanochoerus* and *Libycochoerus* in the Kubanochoerinae, and believed them to be different from the Listriodontinae. Van der Made (1996) considered the genera synonymous and belonging to the Kubanochoerini of the Listriodontinae. In the following, the informal 'kubanochoeres' and 'listriodonts' will be used whenever the taxonomic level is under discussion.

This paper discusses the status of *Eurolistriodon* and the characters that have a bearing on the status of the kubanochoeres in order to answer the question: 'should the kubanochoeres be included in the Listriodontinae or do they consitute a subfamily of their own?'

## ABREVIATIONS OF MEASUREMENTS AND COLLECTIONS

| | |
|---|---|
| DMD | Meso-distal diameter in mm, taken as indicated by Van der Made (1996). |
| DMD' | DMD of an incisors, expressed as a percentage of the width of the M1 ($M^1$ for upper incisors, $M_1$ for lowers). |
| DLL | Labio-lingual diameter in mm, taken as indicated by Van der Made (1996). |
| I | The meso-distal diameter (DMD) expressed as a percentage of the labio-lingual diameter (DLL): $I = 100\ DMD/DLL$ |

| | |
|---|---|
| BNHM | Beijing Natural History Museum. |
| BSPHGM | Bayerische Staatssammlung für Paläontologie und Historische Geologie, München. |
| GSP | Geological Survey of Pakistan, Islamabad. |
| HLD | Hessisches Landesmuseum Darmstadt. |
| IM | Indian Museum, Calcutta. |
| IPS | Institut de Paleontologia, Sabadell. |
| IVAU | Instituut voor Aardwetenschappen, Utrecht. |
| IVPP | Institute for Vertebrate Palaeontology and Palaeoanthropology, Beijing. |
| KNM | Kenya National Museums, Nairobi. |
| MNCN | Museo Nacional de Ciencias Naturales, Madrid. |
| MNHNP | Muséum National d'Histoire Naturelle, Paris. |
| MPZ | Palaeontological Museum of the University of Zaragoza. |
| MTA | Maden Tetkik ve Arama, Ankara. |
| NMB | Naturhistorisches Museum, Basel. |
| NNML | Nationaal Natuurhistorisch Museum, Leiden. |
| PDTFAU | Paleontropoloii, Dil ve Tarih Cografya Facultesi, Ankara Universitesi. |
| SLJG | Steiermärkisches Landesmuseum Joanneum, Graz. |
| SMNS | Staatliche Museum für Naturkunde in Stuttgart. |
| UCBL | Université Claude Bernard, Lyon. |
| ULAR | Universitá La Sapiensa, Rome. |
| ZMA | Zoölogisch Museum, Amterdam. |

## THE STATUS OF *BUNOLISTRIODON*

Arambourg (1933) introduced the name *Bunolistriodon* conditionally for a group of bunodont and sublophodont suids, that at that time were included in *Listriodon*. He did not designate a type species. After 1930, the introduction of a genus should be accompanied by the indication of a type species (International Code of Zoological Nomenclature, article 13b; Ride et al. 1985), also the conditional introduction of a genus. Thus *Bunolistriodon* Arambourg, 1933 is a nomen nudum. A nomen nudum is a not available name that may be made available later, taking authorship and date of that later publication (ICZN).

Arambourg (1961) described a mandible from Gebel Zelten and based the new generic and specific names *Libycochoerus massai* on it. At that moment he considered the genus to be related to *Propotamochoerus* and *Conohyus*. A skull of the same species was found later at Gebel Zelten, as well as a large collection of bones and teeth. This made Arambourg (1963) aware of the similarity between *Libycochoerus* and bunodont listriodonts and he considered *Libycochoerus* Arambourg, 1961 as a junior synonym of *Bunolistriodon* Arambourg, 1933. At this stage Arambourg (1963) designated '*Sus lockharti* Pomel, 1843' as type species of *Bunolistriodon*. It is evident that Arambourg (1963) meant *Sus lockharti* Pomel, 1848, since Arambourg (1933), cited by Arambourg (1963), referred to Pomel (1848). The fact that in 1933 no type species was indicated is thus no reason, why *Bunolistriodon* Arambourg, 1963 should not be available.

Pickford and Moyà-Solà (1995, p. 352) state that Arambourg (1961) described a skull from Libya, which gives the false impression that Arambourg (1961) based *Libycochoerus* on good and abundant material, whereas in reality this additional evidence convinced Arambourg (1963) that the name *Libycochoerus* is a synonym of *Bunolistriodon* and should not be used anymore.

Leinders (1976), Pickford (1995) and Pickford and Moyà Solà (1995) were of the opinion that the name *Bunolistriodon* is not available, for at least one of two reasons: problems with the diagnosis or with the type species. Pickford and Moyà Solà (1995) considered the genus as a nomen nudum and introduced the name *Eurolistriodon* to replace it. The type species of *Eurolistriodon* is *E. adelli*. Two other species are included in the new genus: *B. lockharti*, type species of *Bunolistriodon*, and *B. latidens*. *E. adelli* might be identical with *B.* aff. *latidens* of Van der Made (1996) and we agree that both species (*B. lockharti* and *B. adelli*) belong to the same genus.

Arambourg's (1963) diagnosis of *Bunolistriodon* has been criticized (Leinders, 1975; Pickford, 1993; Pickford and Moyà Solà, 1995). Pickford and Moyà Solà (1995, p. 353) cite Arambourg's (1963) diagnosis completely, underlining characters that they could not observe in *B. lockharti* and underlining double characters that they consider to be primitive.

Though it is common to give a diagnosis with the introduction of a taxon, the word diagnosis is not used in the ICZN. The ICZN (article 13ai) puts it in this way: 'accompanied by a description or definition that states in words characters that are purported to differentiate the taxon'. Thus, the presence or absence or the form and contents of a diagnosis does not affect the availability of a taxon as long as somewhere in the publication characters are mentioned which are meant to make clear how the taxon differs from other taxa. This is exactly what Arambourg (1963) did, he gave characters, meant to differentiate *Bunolistriodon* from *Listriodon*.

Pickford and Moyà Solà (1995, p. 353) cited Arambourg's diagnosis and underlined characters that in their opinion cannot be observed in *B. lockharti* because they are not found in the skull from Els Casots (which is another species!), and double underlined the characters that, in their opinion, are primitive at the family or higher rank. Underlined is 'denture complète', the skull from Els Casots lacks the P2. However, specimens from La Romieu (UCBL) and Langenau (SMNS) show that *B. lockharti* has both the $P^2$ and the $P_2$. 'Région antorbitaire alongée' has double underlining, indicating that the character is considered to be primitive. But the primitive state in Suidae is with a short snout. Anyway, a genus is not invalidated if in differentiating it either primitive characters are used or characters that are observed in species attributed to that genus.

In fact, Pickford and Moyà-Solà (1995) claim that *Bunolistriodon* is not valid, because a species *they* describe does not fit Arambourg's diagnosis: 'These are now known not to occur in the bunodont Listriodontinae as exemplified by the skull from Els Casots.' (p. 353). Taxonomy would become a chaos, if we would introduce new names for old taxa, each time we obtain new information. A simple alternative is to ammend the old diagnosis.

### Conclusions

(1) Bunolistriodon Arambourg, 1933 is a nomen nudum, but *Bunolistriodon* Arambourg, 1963 is available because Arambourg (1963) indicated a type species for *Bunolistriodon* and indicated characters meant to differentiate the genus.

(2) The quality of an original diagnosis does not invalidate a taxon.

(3) Additional morphological information does not invalidate previous taxonomical acts.

(4) The type species of *Eurolistriodon*, *E. adelli* belongs to the same genus as *B. lockharti*, type species of *Bunolistriodon*. Therefore, *Eurolistriodon* Pickford and Moyà Solà, 1995 is a junior synonym of *Bunolistriodon* Arambourg, 1963.

## THE STATUS OF THE 'KUBANOCHOERES'

Pickford and Moyà Solà (1995) placed *Kubanochoerus* in the Kubanochoerinae and not in the Listriodontinae. However, they do not involve *K. gigas*, type species of *Kubanochoerus* in their discussion, but *Libycochoerus* (which they consider to be different from *Kubanochoerus*) and apparently in particular the species *L. massai* as well as material attributed to *L. jeanneli*. Pickford and Moyà-Solà (1995) cite at least 14 characters that they consider to separate kubanochoeres from the Listriodontinae. These characters and two others, not mentioned by them, will be discussed below.

Some of the characters used by Pickford and Moyà Solà (1995) concern the skull. Skull characters are of great importance, but the study of sexual, ontogenetic and individual variation in suid skulls in some large samples in the ZMA and NNML revealed that skull characters may be very variable (Van der

Made, 1991), which makes me cautious in the application of these characters to small samples of fossils. Morphological and metrical characters are much more variable in suid skulls than in suid dentitions.

## 1. Posterior extension of the palate

Citing Gabunia (1960) in support of their observations, Pickford and Moyà-Solà (1995, p. 357) state: 'Listriodonts have posteriorly extended palatines, kubanochoeres do not'. Gabunia (1960, p. 89) described the *Kubanochoerus* skull from Belometchetskaia as follows: 'Le Bord postérieur du palais est très élongé du bord posterieur de la troisième molaire (la distance est à peu près de 90 mm).' A *Kubanochoerus* skull from Tongxin figured by Qiu et al. (1988, fig. 2, plate 2, fig. 1) also shows that the palate extends far behind the $M^3$. The distance measured from the line connecting the posterior limits of both $M^3$ to the anteriormost point of the posterior limit of the palate is 95 mm (IVPP). Some other skulls from Tongxin in the BMHN have the palate broken off at 60, 98 and 105 mm behind the $M^3$. Instead of lacking posterior extension of the palate, as is claimed by Pickford and Moyà Solà, *K. gigas* may well be the suid with the most posteriorly extended palate. But these are absolute values in a large species.

All known skulls of *K. gigas* are male, the sole known skull of *K. massai* is female as indicated by the canines and has a 'short palate'. Could the character be sexually dimorphic, or very variable? What happens if we take general size into account?

Figure 3 shows, that there is not much difference in the distance the palate extends behind the $M^3$ between males and females in species where this distance is small. But the few data of the species where this distance is longer suggest that sexual dimorphism increases when the distance increases. *K. gigas* has $M_1$ that are about twice as long as the $M_1$ of *S. barbatus* and the length of the palate behind the $M^3$ is also about twice as long. $M_1$ size is believed to be related to body size (Legendre, 1986). Relative to its size, *K. massai* has the palate as far behind the $M^3$ as *S. scrofa vittatus*. The degree of variation in extension of the palate behind the $M^3$ in the genus *Kubanochoerus* is comparable to that in the genus *Sus*.

Both 'short' and 'long' palates occur in kubanochoeres. The variation of the character is as in living species of the genus *Sus*. Both absolutely (figure 1) and relatively, the posterior extension of the palate in *L. splendens* (type species of *Listriodon*) is within the ranges of the genus *Kubanochoerus*, therefore the character is no good ground for separating the listriodonts and kubanochoeres into two subfamilies.

## 2. Mesially touching first upper incisors

'Listriodonts have closely apposed premaxillae and the central incisors meet interproximally, kubanochoeres have premaxillae that do not meet anteriorly, neither do the central incisors touch each other.' (Pickford and Moyà-Solà,

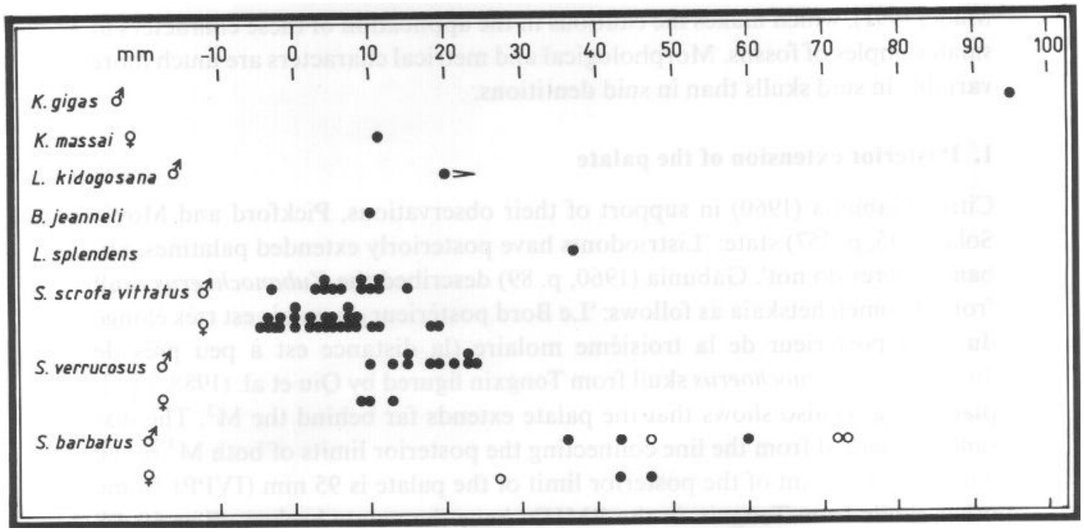

Fig. 3. Extension of the palate behind the $M^3$ in mm. The exact measurement is the shortest distance between the line through the posterior limits of both $M^3$ and the posterior edge of the palate (Van der Made, 1996). Extant male and female *Sus scrofa vittatus* from Deli, Sumatra, Indonesia (ZMA), *Sus barbatus* from east Bulungan, Kalimantan (ZMA) and *Sus verrucosus* from Java (ZMA, NNML). The same samples were used by Van der Made (1991). Fossil: *Kubanochoerus gigas* from Tongxin, China (IVPP), *K. massai* from Gebel Zelten, Libya (holotype: MNHNP), *Lopholistriodon kidogosana* from the Ngorora Formation, Kenya (KNM), *Bunolistriodon jeanneli* from Moruorot, Kenya (holotype; MNHNP), *Listriodon splendens* from Arroyo del Val IV, Spain (IVAU). Open circles for *S. barbatus* indicate approximate measurements. The arrow for *L. kidogosana* indicates a minimum measurement.

1995, p. 358). These two characters are clearly related. Skulls of recent suids in museum collections sometimes have the premaxillae divergent due to dessiccation. The same may have occurred in skulls that became fossilized. It seems more reliable to study presence or absence of mesial wear facets on the $I^1$. This has the additional advantage that the character state can be observed in isolated teeth.

Qiu et al. (1988, plate 3, fig. 1) figured a *Kubanochoerus* premaxilla from Tongxin. In this specimen the $I^1$ developed mesial facets and consequently they must have touched. This material is attributed to *K. gigas* , type species of the genus (Van der Made, 1996).

Primitive Suoidea do not have mesial wear facets on the $I^1$. This can be observed in: Palaeochoeridae, such as *Propalaeochoerus* (several specimens in the SMNS), Cainochoerinae such as *Cainochoerus* from Langebaanweg and *Albanohyus* from Castell de Barberà (material in the IPS), early Hyotheriinae such as *Hyotherium meisneri* and *H. major* (Van der Made, 1994, plate 2, fig. 4c; Hellmund, 1991, plate 7, fig. 1b), early Tetraconodontinae such as *Conohyus* (Thenius, 1956, fig. 20a but not fig. 20cd, which represents *Hyotherium* as indicated by the distal cusp). However, facets are present in later hyotheriines such as *Hyotherium soemmeringi* (Hellmund, 1991, plate 12, fig. 1b). Suinae tend to have mesial wear facets. *Babiroussa* does not have mesial wear facets. It is obvious that the presence of mesial wear facets developed more than once, preferentially in suids with meso-distally enlarged $I^1$. In Listriodontinae (incl. kubanochoeres), the wear facets tend to occur in those species that have large and elongated $I^1$. The more elongated or enlarged the $I^1$, the more important the mesial wear. This suggests that these characters are correlated. With increase in meso-distal diameter of the $I^1$, mesial wear facets started to develop in *Kubanochoerus*.

## 3. Diastema length

'Listriodonts have very long post-canine diastemata, kubanochoeres do not' (Pickford and Moyà-Solà, 1995, p. 358). As Gabunia (1960, p. 90) put it, describing the *Kubanochoerus* from Belometchetskaia: 'Le diasteme assez long'. Distance $C_m$-$P_2$ in *Kubanochoerus gigas* from Tongxin: 60.6, 58.2, 57.4 mm (data from Van der Made, 1996). These are high values.

The application of diastema length in suid taxonomy is not without problems, because it is subject to sexual and individual variation within similar age groups. There is still an important increase in diastema length from subadult (having the M3 not or not completely erupted) to adult males. The increase is most pronounced in the $P_1$-$P_2$ diastema: subadults in a large sample of *S. scofa vittatus* have values of only 68% of the adults. In adult males the diastema length ranges from 1.0 to 12.7 mm, so the variation is enormous. The $C_m$-$P_2$ distance ranges from 13.9 to 22.9 mm. (Data from Van der Made, 1991.) In a smaller sample of male *B. barbatus* the $C_m$-$P_2$ distance is around 25 mm in subadults and 35 in adults. In adult males of *S. verrucosus* this distance varies between 24.3 and 48.1 mm.

The $C_m$-$P_2$ distance in *B. lockharti* from Pellecahus is approximately 55 mm and in *L. splendens* from various localities: 52, 67, 71.5, 71.5 and 71 mm. The $C_f$-$P_2$ distance in the specimen of *L. pentapotamiae* from Dhok Talian is 58.1 and 61.2 mm. After correcting for general size difference, the $C_x$-$P_2$ distance in *K. gigas* would be similar to that of *S. barbatus* and probably significantly shorter than in *L. splendens*. The difference between *Sus verrucosus* and *Sus scrofa vittatus* is of the same magnitude as between *L. splendens* and *K. gigas*.

## 4. Canine flanges

When Pickford and Moyà-Solà (1995, p. 358) stated that 'listriodonts possess important canine flanges, especially in the males, kubanochoeres have much more moderate canine juga', they must have been referring to the skull and the palate of two females of *K. massai* from Gebel Zelten and the skull of a male *Bunolistriodon* from Els Casots.

Canine flanges are sexually dimorphic, they tend to be well developed only in the males. In recent *Potamochoerus* males, the structure is extremely variable. In Listriodontinae the canine flanges are different from those of *Potamochoerus* and tend to be thin structures that cover the canines at the labial side over a considerable length. They tend to break off easily. There are only very few fossil male skulls in which this part is preserved, maybe only five for all Listriodontinae (including the kubanochoeres). Consequently we know the state of this structure in less than 20% of the listriodontine species by about one specimen each and we don't know anything at all about the variability of the character in any of the species. In *Kubanochoerus* from Tongxin (BNHM) the base of the canine flanges is preserved and is not different from that of a skull of *Listriodon* from Xinan (IVPP).

We do not know enough about variation of canine flanges in listriodonts and kubanochoeres to use the character in taxonomy. Canine flange morphology cannot be used in taxonomy ignoring sexual dimorphism. The few available data do not show important differences between kubanochoeres and listriodonts.

## 'Horns'

The males of *Kubanochoerus* have median frontal 'horns' (all specimens known belong to *K. gigas*) and both males and females have a small frontal protuberance above each orbit (the only female skull known belongs to *K. masai*). This character is absent in all other Listriodontinae of which the skull is known.

Pickford (1986, 1988) placed some small bunodont listriodonts in *Libycochoerus* (= *Kubanochoerus*), including *B. jeanneli* and *B. affinis*. I believe these species do not belong to the kubanochoeres. There is no published material that shows that these species share 'horns' or any other derived character with *Kubanochoerus* (of '*Libycochoerus*'). There is however good material that is not yet published, and we have to await publication of this material to end this dispute.

## 6 and 7. Symphysis

'In the mandible, listriodonts have elongated symphyses which are splayed outwards and bent downwards, while in kubanochoeres the symphysis is shorter and not splayed outwards, nor bent downwards to the same degree' (Pickford and Moyà-Solà, 1995, p. 358). In fact, this are two characters: 6) the elongation of the symphysis and 7) the width of the anterior part of the mandible.

Qiu et al. (1988, plate 3, fig. 2) figured the anterior part of the mandible of *Kubanochoerus gigas* from Tongxin. This mandible has incisors that are mesodistally widened and the mandible is wide in order to accomodate them. The anterior part of the mandible of *K. gigas* is relatively wider than in any Hyotheriinae, Cainochoerinae and most Suinae. It is similar to that in *Listriodon*, *Celebochoerus* and *Phacochoerus*.

The anterior part of the mandible in Listriodontinae and in *Celebochoerus* is wide in the species where the incisors have a great meso-distal diameter and where the $C_m$ is large. The six lower incisors form one continuous row and tend to have well developed facets where the incisors touch each other. There is no important $I_3$-$C_x$ diastema. In *Phacochoerus* the mandible is wide, but the incisors not and there are diastemata between them. These facts suggest that large or wide incisors and large canines are one but not the only cause of a wide anterior part of the mandible.

With regard to the width of the anterior part of the symphysis Pickford and Moyà-Solà (1995) based themselves on specimens which they place in *Libycochoerus*. Whereas it can be disputed whether these symphyses are wide or not, wide symphyses in the type species of *Kubanochoerus* are a fact. The evolutive significance of the character is related to that of the width of the incisors, a character that is discussed below.

The length of the symphysis is subject to great individual, sexual and ontogenetic variation. Figure 4 presents data on symphysis length of the same samples of recent suids that have been mentioned before. Within one group of similar age and sex, differences may be over 40%. Whereas average sizes between males and females in the same samples differ 3% in the teeth (Van der Made, 1991), differences in size between males and females in the same age group may be over 20%. Differences between subadults and adults of the same sex may be of the same order. Symphysis length should be used with care, certainly when samples are small.

A symphysis of *K. gigas* from Tongxin in the IVPP has a length of 145.5 mm and the symphysis of a male *L. splendens* from Çandir 107.5 mm. If we correct for the size difference of these species, the difference is similar to the difference between the averages of adult males of *S. scrofa vittatus* and *S. verrucosus* or between extreme values of males of one sample. We do not know the variation of this character in any of the fossil species. I could measure the character in

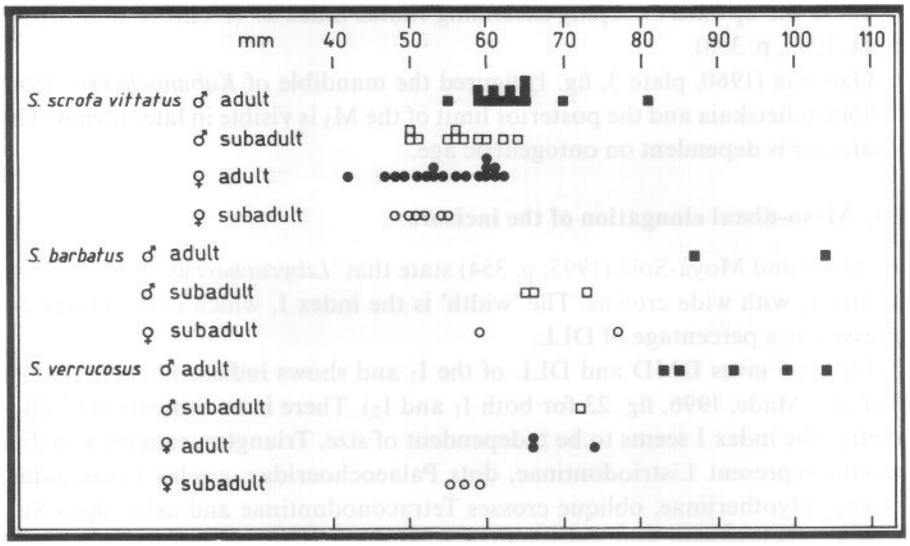

Fig. 4. Symphysis length in mm for three extant species of suids. Indicated is the distance from the posterior limit of the alveolus of the $I_1$ to the posterior limit of the symphysis. The same samples as in figure 1. Samples divided in female subadults, female adults, male subadults and male adults. Adults have the $M_3$ fully erupted, subadults have the $M_2$ fully erupted, but the $M_3$ not fully erupted.

5 specimens, two kubanochoeres and three listriodonts, never more than one specimen per species (Van der Made, 1996) and there is probably not much more material available. In these conditions, the character has very limited value.

### 8. The position of the foramen mentale

'The mental foramina occupy different positions in the two subfamilies, below the rear of the $P_4$ in kubanochoeres and below the front of $P_3$ in listriodonts.' (Pickford and Moyà-Solà, 1995, p. 358). This seems to be based on Pickford's (1986) comparison of one mandible of *Listriodon pentapotamiae* and one mandible of *'Libycochoerus jeanneli'* from Rusinga (=*Bunolistriodon anchidens*).

Gabunia (1960, p. 90) indicated that there are several foramina in the specimen of *Kubanochoerus* from Belometchetskaia, the more important ones being below the anterior part of the $P_4$. The type specimen of *K. massai* figured by Arambourg (1961, fig. b) has the foramen below the rear of the $P_3$.

The character is probably variable, and we should avoid drawing far reaching conclusions on small samples, certainly without a study of variability in recent samples.

### 9. Ascending ramus of the mandible

'Furthermore, the ascending ramus of the listriodonts is far back, not hiding the $M_3$ in lateral view, while in kubanochoeres it takes root further forwards on the mandible, so that the rear of the third molar is not visible in lateral view because the upward sweeping ascending ramus hides it.' (Pickford and Moyà-Solà, 1995, p. 358).

Gabunia (1960, plate 3, fig. 1) figured the mandible of *Kubanochoerus* from Belometchetskaia and the posterior limit of the $M_3$ is visible in lateral view. The character is dependent on ontogenetic age.

### 10. Meso-distal elongation of the incisors

Pickford and Moyà-Solà (1995; p. 354) state that '*Libycochoerus*' does not have $I_1$ and $I_2$ with wide crowns. The 'width' is the index I, which is the DMD expressed as a percentage of DLL.

Figure 5 gives DMD and DLL of the $I_1$ and shows indices 80 and 100 (see Van der Made, 1996, fig. 23 for both $I_1$ and $I_2$). There is no indication of allometry: the index I seems to be independent of size. Triangles, squares and diamonds represent Listriodontinae, dots Palaeochoeridae, circles Tayassuidae, crosses Hyotheriinae, oblique crosses Tetraconodontinae and asteriskses Suinae. Paleochoeridae and Tayassuidae apparently tend to have values around 80, Suidae like the Tetraconodontinae and Suinae have usually values between 50 and 80, Hyotheriinae tend to have similar values, save for the species *H. meisneri*. Values are above 100 in *Listriodon* and tend to be above 80 in *Ku-*

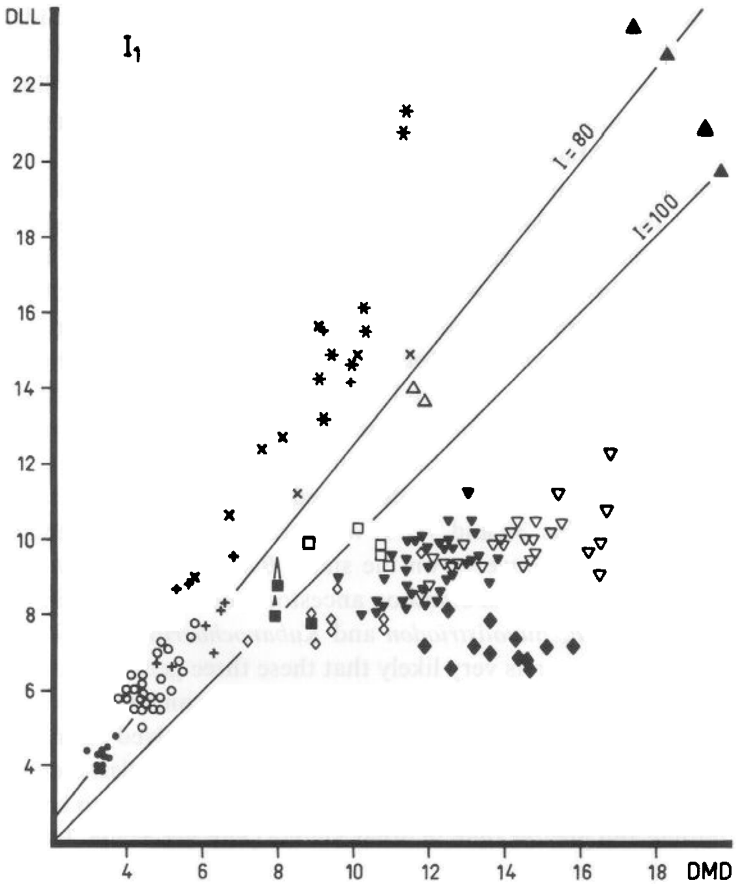

Fig. 5. Bivariate plot of the $I_1$. The lines indicate indices of 'meso-distal elongation' I = 100 DMD/DLL. Dots = *Propalaeochoerus* from Tomerdingen (SMNS), Palaeochoeridae. Circles = white lipped and collared peccary (ZMA), Tayassuidae. Crosses = Hyotheriinae: *Aureliachoerus aurelianensis* from Artenay (NMB), *Hyotherium meisneri* from Cetina (MNCN), *H. soemmeringi* from Sandelzhausen (BSPHGM) and *Xenohyus venitor* (MNHNP). Oblique crosses = Tetraconodontinae: *Conohyus simorrensis* from Göriach (SLJG), from Paşalar (PDTFAU) and Mira (IPS), *Nyanzachoerus waylandi* from Nyaburogo (coll. Pickford), *N. syrticus* from Sahabi (ULAR) and *N. prior* (IM). Asterikses = Suinae: *Hippopotamodon antiquus* from Eppelsheim and Sinap (HLD; MNHNP) and *H. sivalense* (IM).

*banochoerus*. What Pickford and Moyà-Solà (1995) call *Libycochoerus* is represented by open triangles pointing upwards, with an index between 80 and 100 (*K. massai*) and black squares (*Bunolistriodon* from Rusinga). The crowns of the incisors of '*Libycochoerus*' are evidently wider than those of the Tetraconodontinae, Suinae and Hyotheriinae of similar size. Of course, the '*Libycochoerus*' sample is small and in a larger sample some specimens are likely to have an index lower than 80, as is the case in the *K. gigas* sample, but any sample has its variation. The available data show that the indices in the kubanochoeres are on average higher than in other suoids, contradicting the statement of Pickford and Moyà Solà (1995).

Incisors with a great meso-distal diameter occur also in other suids, for instance *Celebochoerus*. *Celebochoerus* is currently placed in the Suinae and its wide incisors evolved convergently, but have high crowns, wheras those of the listriodonts have low crowns. The lower incisors of these suids are discussed elsewhere (Van der Made, 1996).

In several listriodotine lineages incisor width increased parallel, but in a different way. In *B. lockharti* there seems to have been an increase in size, but not in index of the lower incisors and not or a little in the index of the $I^1$ (Van der Made, 1996, figs. 35 and 41). In *Kubanochoerus* the index I of the $I^1$ increased, but the $I_1$ increased in size, but not in index I (figure 5; Van der Made, 1996, fig. 27). In *Listriodon splendens* the meso-distal and labio-lingual diameters increased as well as the index in $I^1$, $I_1$ and $I_2$ (figure 5; Van der Made, 1996, figs. 44 and 47). In the *B. latidens* lineage, the $I^1$ increased in meso-distal diameter, labio-lingual diameter and in index, but the $I_1$ and $I_2$ increased in mesio-distal diameter and index and decreased in labio-lingual diameter (fig. 5; Van der Made, 1995, figs. 35 and 37). If we extrapolate these tendencies in the different lineages, they converge on the small *Bunolistriodon anchidens* from Rusinga. This form is an ideal common ancestor, both in age and in morphology, for all *Listriodon*, *Bunolistriodon* and *Kubanochoerus*, save for *B. affinis* which is still older. It seems very likely that these three genera shared the first stages of meso-distal widening of the incisors, then became separate and, having similar genes responding to similar environments, evolved parallel.

An additional argument for the increased meso-distal diameter in *Kubanochoerus* is the fact that the DMD' of the lower incisors tends to be similar to Listriodontinae and greater than in other Suidae (Van der Made, 1995, fig. 24).

## 11. Height of the crown of the incisors

Pickford and Moyà-Solà (1995, p. 354) state that *Libycochoerus* (exemplifying all kubanochoeres) does not have low crowns.

The height of the crowns of the $I_1$ and $I_2$ increased in many suid lineages. Relative height of crowns is ideally expressed as an index of the height and either the DMD or DLL. In all Listriodontinae, the meso-distal diameter increased and in at least some, the labio-lingual diameter decreased (Van der Made, 1996). As a consequence, a hypsodonty index cannot be used in a simple manner. But since a change in index I of the incisor would cause one index to increase whereas the other would decrease, some idea of the changes can be obtained. It is possible that Listriodontinae actively decreased the height of the crowns. The index of lingual heigth of the crown and DMD and DLL is 166 and 154 respectively in the $I_1$ of *Kubanochoerus minheensis* and 195 and 184 in a primitive suid like *Hyotherium meisneri* and 110 and 160 in one and 153 and 195 in another $I_1$ of *L. splendens* (Van der Made, 1996, table 18).

Where as it is obvious from these data that both *Kubanochoerus* and *Listriodon* may have had incisors with equally low crowns, more data are needed to really prove that crown height decreased in these suids.

## 12. Position of a sulcus in the first upper incisor

Pickford and Moyà-Solà (1995) state that the $I^1$ of kubanochoeres have a sulcus nearly in the middle of the crown, whereas listriodonts have several sulci in the mesial third. The $I^1$ of *Listridon* tends to be divided into two lobes, separated by a major sulcus, any additional sulci disappear with little wear. The ratio of the meso-distal diameters (DMD) of the distal lobe and of the whole crown is 50% when the sulcus is in the middle and 67% when it is in the mesial third.

Figure 6 gives the DMD of the distal lobe as a percentage of the DMD of the whole crown in *Kubanochoerus gigas* as well as in *Listriodon*. It is obvious that there is a great variation, even in a single locality. This is partially due to mesial wear of the tooth and limits the practical use of the character. Extreme values of *Listriodon* are below 55% and available values for *K. gigas* are nearly as high as 70%. The data show that there is no real difference between *K. gigas* and *Listriodon*. Since there is no mesial wear in *K. massai* incisors, the values would tend to be slightly closer to 50%. This, however, is an artifact.

## 13. The presence of a sulcus in the lower incisors

The $I_1$ and $I_2$ of *Kubanochoerus* have a sulcus at the tips of their crowns. According to Pickford and Moyà-Solà (1995), listriodonts do not have this character. However, the character can be observed in the type material of *Listriodon splendens* (type species of *Listriodon*) from La Chaux-de-Fonds.

## 14. Paleodistribution

'The complete lack of overlap in their palaeodistributions provides further evidence that the genetic pools of the kubanochoeres and bunodont listriodonts probably had negligible opportunities to mix, even from the outset of their di-

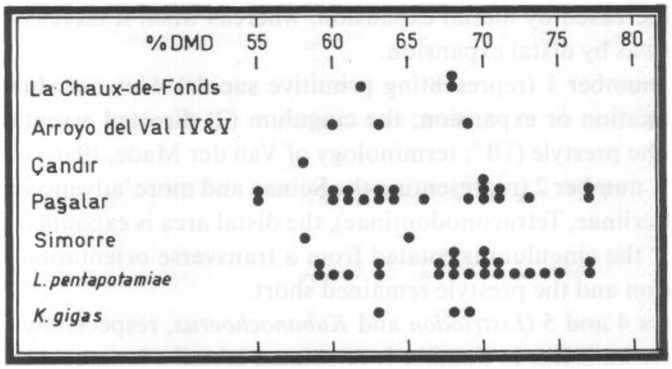

Fig. 6. Relative size of the distal lobe in the $I^1$ expressed as a percentage of the DMD of the whole tooth in *Listriodon* and *Kubanochoerus*. *Listriodon splendens* from Simorre, France (MNHNP), Paşalar, Turkey (PDTFAU, MTA), Çandir, Turkey (PDTFAU, MTA), Arroyo del Val, Spain (IVAU, NNML, MPZ), *L. pentapotamiae* from many localities in Pakistan and India (GSP, IM) and *Kubanochoerus gigas* from Tongxin, China (IVPP, BNHM).

vergence.' (Pickford and Moyà-Solà, 1995, p. 358). This contrasts with an earlier opinion by Pickford (1993, p. 246): 'In fact, during much of the middle Miocene, southern and central Europe, southern Asia, India and Africa belonged to a single biogeographic realm, and there was probably rather free gene flow between these areas throughout the period that listriodonts survived there.' Anyway, different species are not supposed to interbreed, leave alone genera, tribes and subfamilies.

Apart from the question of interbreeding, Pickford and Moyà-Solà (1995) seem to ignore the co-occurrence of *Bunolistriodon* and *Kubanochoerus* in the same localities: Tongxin (Ye et al., 1992), Koujiacun (Liu and Lee, 1963a, b), Inönü I (Pickford and Ertürk, 1979) and in Pakistan (Van der Made, 1996). Not agreeing to place species like *Bunolistriodon jeanneli* from Africa in '*Libycochoerus*', one finds a substantial geographical overlap of *Bunolistriodon* and *Kubanochoerus* in Africa.

## 15. First upper incisors forming a straight crest

The two $I^1$ form a straight transverse crest in the Listriodontinae, whereas they form a 'V-shape' in most other Suidae (Van der Made, 1996). Figure 7, number 1 shows the incisors of a suid that is primitive in this respect; the incisors are not elongated. Number 2 shows incisors that are distally expanded and that have the 'V-shape'. This type is common in Suinae, but occurs also in some Hyotheriinae and Tetraconodontinae. Number 4 shows the incisors of *Listriodon splendens* and number 5 those of *Kubanochoerus gigas*. The incisors of the latter two species form a straight transverse crest. In this character, *Kubanochoerus* is in great detail similar to *Listriodon*.

## 16. Place of meso-distal expansion of the first upper incisor

The meso-distal diameter of the $I^1$ of the Listriodontinae, including *Kubanochoerus*, increased by mesial expansion, whereas when it increased in other Suidae, this was by distal expansion.

Figure 7, number 1 (representing primitive suoids) does not show any important elongation or expansion; the cingulum (2) directed essentially transversely and the prestyle (1B″; terminology of Van der Made, 1996) is short.

In figure 7, number 2 (representing the Suinae and more 'advanced' members of the Hyotheriinae, Tetraconodontinae), the distal area is expanded compared to number 1, the cingulum is rotated from a transverse orientation towards a distal direction and the prestyle remained short.

In numbers 4 and 5 (*Listriodon* and *Kubanochoerus*, respectively) the distal part of the crown is like in number 1, or rotated labially, but not expanded and the cingulum is oriented transversely. The main cusp (1) is elongated and mesially a preconule (1B′) is formed, separated from the main cusp by a sulcus. The prestyle (1B″) is elongated and runs along the base of the preconule in the same way as the cingulum. The place where the prestyle meets the cingulum, is marked by an open angle between the two structures. The elongate listriodont

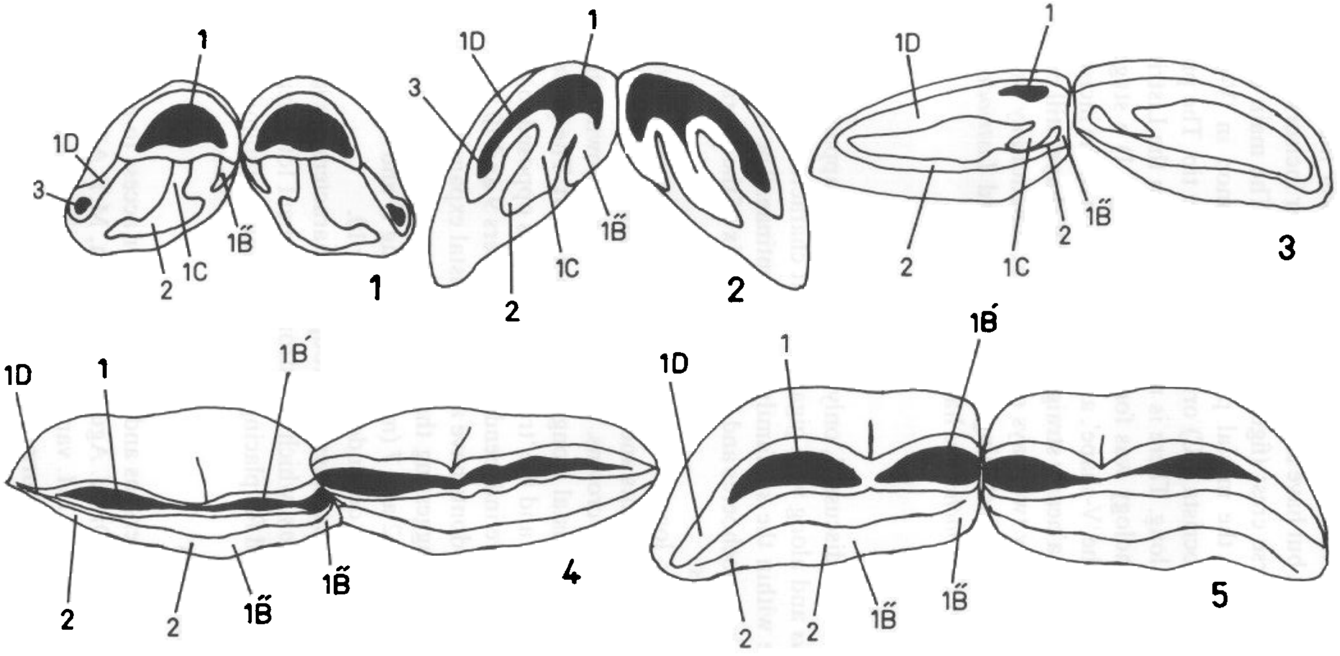

Fig. 7. Terminology of the first upper incisor after Van der Made (1996). 1 = principal cusp (paracone), 1B′ – preconule, 1B″ = prestyle, 1C = endocrista, 1D = postcrista, 2 = cingulum, 3 = distal cusp (metacone). The following taxa are represented: 1) *Conohyus* (representing a primitive incisor type), 2) *Propotamochoerus* (representing the 'V-type'), 3) *Celebochoerus* (modified 'V-type'), 4 *Listriodon* and 5) *Kubanochoerus* (both forming a transverse crest).

morphology resulted from mesial expansion of the tooth, forming immediately a straight crest.

In *Celebochoerus*, which is no listriodont, the lower incisors are wide as in the Listriodontinae, but have high crowns. The upper incisors of *Celebochoerus* form also a transverse crest (figure 7, number 3). The main cusp (1) is positioned very close to the mesial plane, as is common in 'V-shape-incisors' (number 2). The endocrista (1C) originates from the tip. The prestyle is short and the cingulum is long. There is no preconule as in the Listriodotinae. The *Celebochoerus* morphology was formed in two stages 1) a stage of distal expansion resulting in the 'V-shape', and 2) the rotation of the incisors, so that the 'V-shape' turned into a nearly straight crest; the 'V-shape' still can be noted.

There are apparently two ways of arriving at functionally similar upper incisors: *Kubanochoerus* (including *Libycochoerus*) and *Listriodon* have the listriodont type and *Celebochoerus* has the 'suine' type.

## CONCLUSION

Of the 16 characters discussed, only the fifth (cranial appendages) is unique to *Kubanochoerus* and along with gigantic size it characterizes the Kubanochoerini as a tribe within the subfamily Listriodontinae. The other 15 characters occur in both kubanochoeres and listriodonts. Six of the characters are rare or absent in other suids.

*Celebochoerus* has lower incisors with great meso-distal width and high crowns, whereas listriodonts and kubanochoers have incisors with great meso-distal diameters and low crowns. This shows that low crowns (character 11) are independent of meso-distal elongation (character 10). The place of expansion of the $I^1$ (character 16) and the 'transverse crest' as opposed to the 'V-shape' in the $I^1$ (character 15) are independent of characters 9 and 10 as exemplified by *Celebochoerus*. Listriodonts have also some distal expansion but do not have a 'V-shape' in the $I^1$, suggesting that these characters are also independent of each other. Characters 2 and 7 (mesially touching $I^1$ and width of the anterior part of the mandibe) are dependent on character 10.

Three independent characters or groups of characters are shared by *Kubanochoerus* and *Listriodon*, which is a strong argument for considering them as very closely related and for placing them in the same subfamily.

## ACKNOWLEDGEMENTS

I thank the following persons and institutions for access to material and practical or financial help: Drs. J. Agustí, B. Alpagut, M.T. Alberdi, L. Alcalá, M. Arif, B. Azanza, Basu, P.J.H. van Bree, H. de Bruijn, Chen Guangang, B. Engesser, Ç. Ertürk, L. Ginsburg, C. Guérin, E. Güleç, K. Heissig, E.P.J. Heizmann, J.E. van Hinte, S. T. Hussain, Juan Jian, T. Kotsakis, M. Leakey, J. Morales, S. Moyà Solà, M. Munngu, R. Niederl, G. Saraç, F. Schrenk, C. Smeenk, P.Y. Sondaar, E. Ünay, Ye Jie, the Netherlands Foundation for the

Advancement of Tropical Research (WOTRO), Shell Nederland BV and the Government of Kenya.

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